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Egg Development Timing for Riverine Spawning Pygmy Whitefish (*Prosopium coulterii*)

Abstract

Despite the large numbers of individuals present during riverine broadcast spawning, little is known about the spawning behavior or egg development timing of pygmy whitefish (*Prosopium coulterii*). We captured pygmy whitefish from spawning schools in the upper Cedar River, Washington State, and live-spawned to collect milt and eggs. Once fertilized, eggs were placed in Whitlock-Vibert incubation boxes in natural river conditions until hatching. Egg development was monitored weekly by counting eggs and alevin present in boxes, examining a previously undisturbed box each week. Pygmy whitefish hatched over a range of 324 to 370 accumulated temperature units (ATUs). The range in hatch times in this population may be a result of multiple selection pressures (e.g., high flow events frequency, predation, food availability) that confer differing advantages to early and late-hatching individuals. Consequently, even though all broadcast spawning occurs within two weeks, hatching and emergence is spread over a broader temporal period so that not all individuals in the cohort are subjected to the same environmental conditions. These results give better understanding of the timing of hatch and emergence in a pygmy whitefish population and contribute to better management of the species in the face of environmental uncertainty resulting from global climate change.

Introduction

Pygmy whitefish (*Prosopium coulterii*) are a glacial relict species that reside in the deepest portions of large lake systems in the upper Midwest and western United States, western Canada, and into Alaska. In Washington State, the species is currently found in only nine of fifteen historically occupied lakes (Hallock and Mongillo 1998). Pygmy whitefish and other relatives in the whitefish family are important forage fish to larger predatory species, such as bull trout (*Salvelinus confluentus*), and are thus critical components in the trophic structure of some freshwater ecosystems (Weisel et al. 1973, Connor et al. 2001, Witt et al. 2011). Relatively little is known about habitat use by the species but repeated sampling with gill nets in a Canadian lake indicated that pygmy whitefish are most often found along the bottom of the lake (Zemlak and McPhail 2006).

Pygmy whitefish are broadcast spawners and deposit eggs in riverine habitat, generally over cobble and gravel substrate (Hallock and Mongillo 1998). Chester Morse Lake (CML), a municipal water supply reservoir for the City of Seattle within the central Cascade Mountains of western Washington, supports a population of pygmy whitefish that resides in the reservoir for the majority of the year and utilizes two major tributaries to spawn early each winter.

Although lake spawning is known to occur in some pygmy whitefish populations (Zemlak and McPhail 2004), lake spawning is not known to occur in the CML population, and future recruitment depends on successful incubation and emergence from riverine habitat. Fecundity data indicates that female pygmy whitefish in CML produce from 192 to 1412 eggs (Wydowski and Whitney 2003).

The spatial and temporal distribution of spawning schools in the Cedar and Rex rivers has been monitored annually from 2001 through 2011 (Seattle Public Utilities [SPU], unpublished data). In general, large schools of pygmy whitefish move into the two rivers at the beginning of December after stream temperatures fall below 5 °C. Schools of fish are consistently observed in relatively low

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flow habitats classified as a glide or pool tailout. Most commonly, pygmy whitefish spawning schools were observed holding over small to large sized gravel (32 mm to 90 mm), but some schools were found over much finer substrates, including sand. Pygmy whitefish in breeding condition have been documented in other populations in late November (Eschmeyer and Bailey 1955, Heard and Hartman 1966).

Pygmy whitefish are especially important in the trophic structure of CML, as they are one of the primary prey for adfluvial bull trout, a species listed as threatened under the U.S. Endangered Species Act. The fish community in CML is composed of only four species: bull trout, pygmy whitefish, rainbow trout (*Oncorhynchus mykiss*) and shorthead sculpin (*Cottus confusus*). Bull trout are largely piscivorous (Beauchamp and Van Tassell 2001) and diet samples from individuals collected in CML indicate that pygmy whitefish are consumed throughout the year (Connor et al. 2001). The population of pygmy whitefish in CML contributes to maintaining a healthy bull trout population.

Little is known about the early life history of pygmy whitefish in the Pacific Northwest, and almost no information is available for early stages between spawning and larval emergence (Hallock and Mongillo 1998). Several studies have reported hatching time for lake whitefish (*Coregonus clupeaformis*) under laboratory conditions, a species with a similar life history to the pygmy whitefish (Price 1940, Brooke 1975). Although many broadcast spawning species deposit eggs in warmer water (e.g., redside shiner [*Richardsonius balteatus*]), pygmy whitefish and lake whitefish spawn during the coldest time of the year and require substantial egg development time in the gravel before hatching. Brooke (1975) found that lake whitefish hatched under controlled laboratory conditions after approximately 81.5 days at 5.9 °C (81.5 x 5.9 = 480.9 accumulated temperature units [ATUs]) and 111.5 days at 4.0 °C (446 ATUs). In another study, hatching time for lake whitefish incubated in the laboratory at 6 °C was determined to be roughly 58 days or 348 ATUs (Price 1940), whereas Wydowski and Whitney (2003) report hatching in one month at 10 °C (310 ATUs). The primary goal of this study was to determine time to hatching for pygmy whitefish eggs developing under natural riverine flow and temperature conditions in the Cedar River, providing a range of ATUs to hatching that can be applied to other riverine spawning populations to better understand the early life history of the species.

Study Area

Chester Morse Lake is located within the Cedar River Municipal Watershed (CRMW) in the central Cascade Mountains, approximately 55 km east of Seattle, Washington (Figure 1). The CRMW is owned by the City of Seattle and is one of the primary watersheds providing the City's water supply. Since 2000, aquatic and terrestrial resources in the watershed have been managed under a Habitat Conservation Plan (City of Seattle 2000) to ensure compliance with the federal U.S. Endangered Species Act. Before its use as a municipal water supply, CML was a natural lake (previously known as Cedar Lake) with an outlet elevation of 467.1 m (above mean sea level). Construction of the Masonry Dam in 1915 increased the capacity of the reservoir to a maximum water elevation of 478.7 m, although water levels are typically maintained below 477.1 m. The surface area of CML is approximately 7.0 km^2 at full pool elevation of 476.4 m. The majority of the main lake basin has steep slopes extending to the bottom of the lake creating depths of 30 - 35 m throughout much of the main reservoir. Daily temperature profiles collected in the deepest portion of the reservoir indicate that bottom temperatures maintain between 5 – 6 °C throughout the year with a thermocline occurring at approximately 15 m during summer months. A natural falls barrier downstream of the Masonry Dam prohibits access to CML by anadromous fishes and has isolated the pygmy whitefish and bull trout populations since glacial times.

The Cedar and Rex rivers flow into CML from the east and provide low gradient spawning habitat for pygmy whitefish, as well as for bull trout and rainbow trout. Bull trout spawn during fall months (typically October through early December) and rainbow trout spawn in early spring

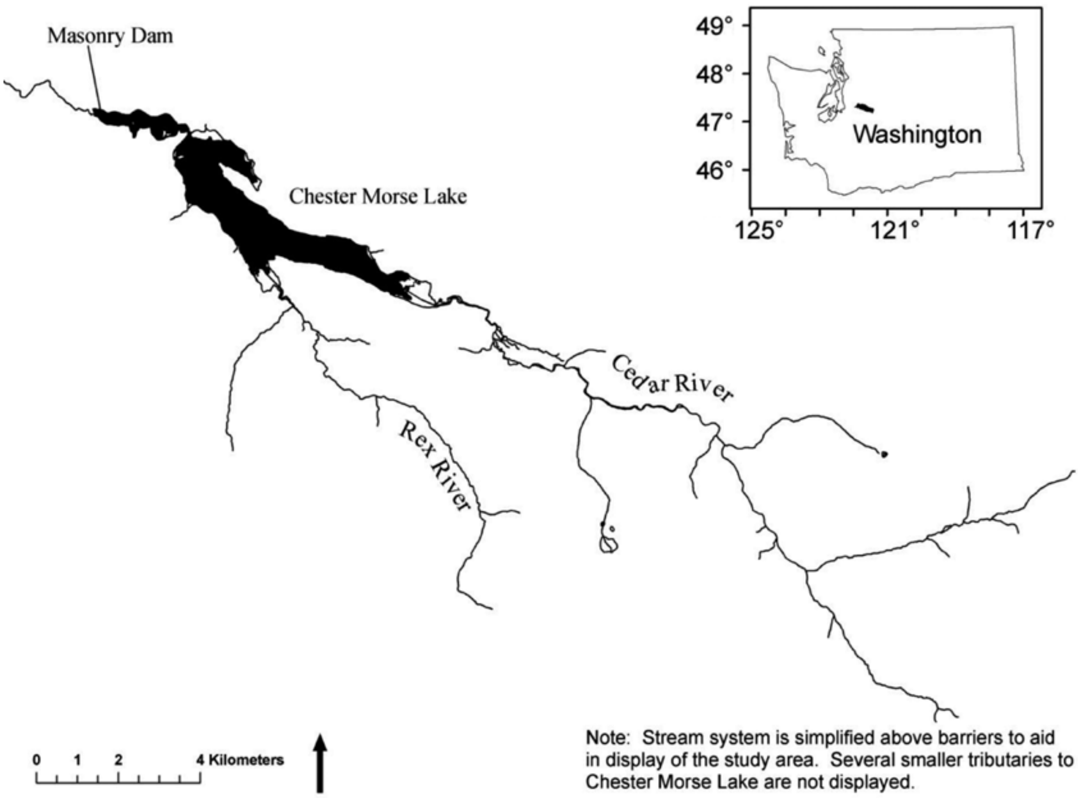

Figure 1. Location of Chester Morse Lake, and the Cedar and Rex rivers in the upper Cedar River Municipal Watershed used by pygmy whitefish for spawning. Stream network is simplified for display purposes.

(March through May) (SPU unpublished data). Spawning surveys for pygmy whitefish indicate that the majority of activity occurs in the first two weeks of December (SPU unpublished data). The amount of accessible stream available to all species totals approximately 24 and 6 km, respectively, in the Cedar and Rex rivers. Despite access to habitat, both pygmy whitefish and bull trout are found using the first 3.4 and 1.7 km upstream of CML on the Cedar and Rex rivers, respectively, for spawning. Rainbow trout also spawn in this reach of river, but spawning activity is much more widely distributed in the watershed. Both river systems average less than one percent gradient in approximately the first 2.0 km upstream of the reservoir. All other minor tributaries entering CML directly increase steeply in gradient from the reservoir and do not provide the type of habitat used by riverine spawning pygmy whitefish in this system (Figure 1).

Methods

Fish Capture and Live-spawning

We captured pygmy whitefish with beach seines on 11 December 2007, in the Cedar River approximately 750 m upstream of CML. A single spawning school was captured, gender was determined, and fish were transferred to holding pens placed in pools in the river before further handling. Females were placed into a separate holding tub before live spawning. Past experience collecting pygmy whitefish showed that females are ripe upon entering the rivers and easily release eggs.

Whitlock-Vibert boxes (W-V boxes) were modified to hold the tiny pygmy whitefish eggs (~2 mm diameter) during incubation by securing nylon window screening inside each box with hot glue. Each box was numbered with an internal and external tag to allow unique identification. All W-V boxes were filled with clean gravel characteristic of the sizes pygmy whitefish spawning schools are observed over in the Cedar River. A one-meter length of colored twine tied to a corner of the box allowed for identification in the river. A total of 20 boxes were prepared.

A few eggs were gently stripped from 24 females into a clean container until approximately 40 ml of eggs were collected. Many of the females were partially spawned before capture and did not provide high numbers of eggs. Milt from six randomly selected males was added to the eggs and gently swirled in the container to promote fertilization, and no effort was made to keep eggs or milt from individual fish separate. The eggs and milt circulated for several minutes before eggs were gently transferred to a larger bucket of clean river water to water harden. Eggs water-hardened for one hour before they were transferred to the W-V boxes. Approximately 1.2 ml of eggs was measured into each box with a measuring spoon because pygmy whitefish eggs are too small and delicate to individually count. Additionally, eggs adhered quickly to surfaces they contacted after fertilization making handling individual eggs impossible. A sample of surplus eggs was taken back to the lab and twelve representative scoops were carefully counted. Results from these counts showed an average of 59 fertilized eggs (SD = 7.0) were added to each W-V box in the study. While the success rate of egg fertilization is unknown, cautious and consistent procedures and abundant supply of milt likely resulted in most eggs being fertilized successfully.

The test site was selected based on repeat sightings of pygmy whitefish spawning schools over several seasons. Three shallow trenches (25 cm depth) were dug in the gravel substrate perpendicular to flow in a low gradient riffle. The W-V boxes (six to seven per trench) containing fertilized eggs were placed approximately 15 cm apart so that the overall design created a square grid with all boxes equal distance apart. W-V boxes were then covered shallowly with native substrate to simulate eggs settling into substrate. A single box was removed each week beginning 34 days and ending 151 days after the egg boxes were initially placed (Table 1). A W-V box was selected at random from the most downstream trench in the grid beginning Day 34. Once all boxes in the downstream trench were checked, boxes from the second most downstream trench in the grid were selected for weekly monitoring. After gently dislodging the box, it was placed in a tray holding a small amount of river water. The substrate contents of the box were carefully sorted with dissecting tweezers. Each pebble was examined, as some pygmy whitefish eggs adhere to surfaces throughout development, and all remaining sand was carefully sifted to count each egg and assess its developmental condition. Data collected included the number of live and dead eggs, number of egg membrane pieces, number of alevin present, notes on developmental stage of eggs, and weekly photo documentation.

Temperature Monitoring

A temperature logger (HOBO logger, Onset Corporation, Pocasset, MA) was installed at the study site to collect stream temperature continu-

TABLE 1. Weekly monitoring results of pygmy whitefish incubation study in the Cedar River, Washington.

Date	Day of study	No. of eggs	No. of membranes	No. of alevin
12/11/07	0	27		
1/10/08	30	31		
1/18/08	38	32		
1/25/08	45	31		
2/3/08	54	27		
2/8/08	59	28		
2/15/08	66	26		
2/21/08	72	40		
2/28/08	79	35	3	
3/5/08	85	33	6	
3/12/08	92	24	3	
3/19/08	99	34	3	
3/25/08	105	29		
4/1/08	112	31	2	
4/8/08	119	32	1	
4/16/08	127	11	4	1
4/23/08	134	22	2	9
4/30/08	141	3	3	1
5/6/08	147	0	0	0

ously. Stream temperature was recorded every 90 min throughout the study. These data provided the basis for determining ATUs to hatch in this study. In addition, stream temperature is collected at a real-time USGS streamflow-gaging station (12115000) 100 m downstream of the study site. Stream temperatures from this real-time site for years 2004 - 2007 were used to assess inter-annual variability in potential hatch timing for pygmy whitefish in the Cedar River. Average daily temperature data were plotted to determine the number of days needed to reach the estimated ATU range.

Results

Egg Box Monitoring

Weekly monitoring of egg boxes on Days 30, 38, and 45 (81 – 115 ATUs) after fertilization indicated that approximately 27 to 32 eggs (46 to 54 % of average egg number per box) survived to continue incubating (Figure 2). It is likely that the eggs not accounted for (approximately 50 percent) were damaged during transfer from water hardening to the egg boxes and subsequently degenerated. Pygmy whitefish eggs were first observed at the eyed stage on Day 38 (100 ATUs) of the study.

From Days 54 to 79 (127 – 179 ATUs) after fertilization, totals of between 26 to 40 eggs were found incubating during weekly checks of egg boxes. All eggs were eyed and embryos were observed moving inside of eggs. By Day 79 (179 ATUs), the eyes were well developed and details of coloring and pupils could be seen easily without magnification. Most eggs adhered to pebbles in the boxes, but a few settled deeper in the box between the gravels and did not adhere to any substrate. In many cases, tiny sand particles were stuck to the outside of the live eggs. On Day 79, pieces of egg membrane from three different eggs were present suggesting that a few individuals might have hatched, however no alevin were observed (Figure 2).

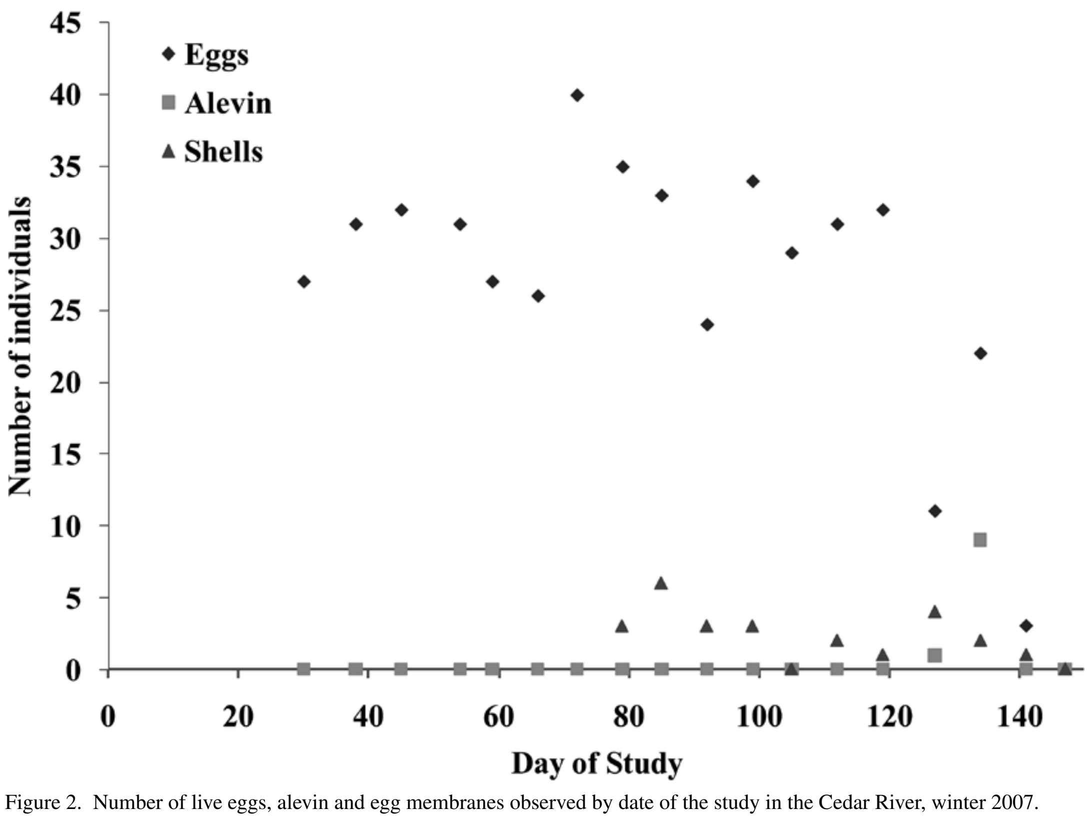

Figure 2. Number of live eggs, alevin and egg membranes observed by date of the study in the Cedar River, winter 2007.

Eggs continued to develop between Days 85 and 105 (197 – 258 ATUs) after fertilization, and embryos were extremely active inside eggs when disturbed. Although alevin were not documented, egg membranes were found indicating that some hatching occurred during this time period. On Day 105 (258 ATUs), ten live eggs were transported back to the lab for examination under the microscope. Within two hours, eight of the ten eggs hatched in the transport container and larval fish were actively swimming. The average total length of larval fish on Day 105 was 12.5 mm.

Examination of egg boxes from Day 119 to Day 141 (297 – 370 ATUs) provided the most definitive evidence of hatching in the study. On Days 112 and 119, 31 and 32 eggs, respectively, were counted in boxes, but by Day 127 the number of live pygmy whitefish eggs remaining in a box dropped by two-thirds. One live alevin was observed in the box on Day 127 (324 ATUs), the first observation of an alevin during the study. On Day 134 (346 ATUs), 22 live eggs and nine live alevin were counted in a box indicating that many eggs were hatching. One week later on Day 141 (370 ATUs) no live eggs and five alevin were found. Similar results were observed on Day 147 (393 ATUS) of the study when one live egg and one live alevin was counted in the egg box (Figure 2). Since many alevin were unaccounted for, it was concluded that they escaped through the mesh screening on the inside of W-V boxes once yolk sacs were slightly absorbed.

Accumulated Temperature Units to Emergence

The winter of 2007 provided some of the coldest stream temperatures on recent record (Figure 3). Stream temperature on Day 1 of the study averaged 2.7 °C and dropped to a low of 0.7 °C on Day 66. Temperatures began to rise steadily after Day

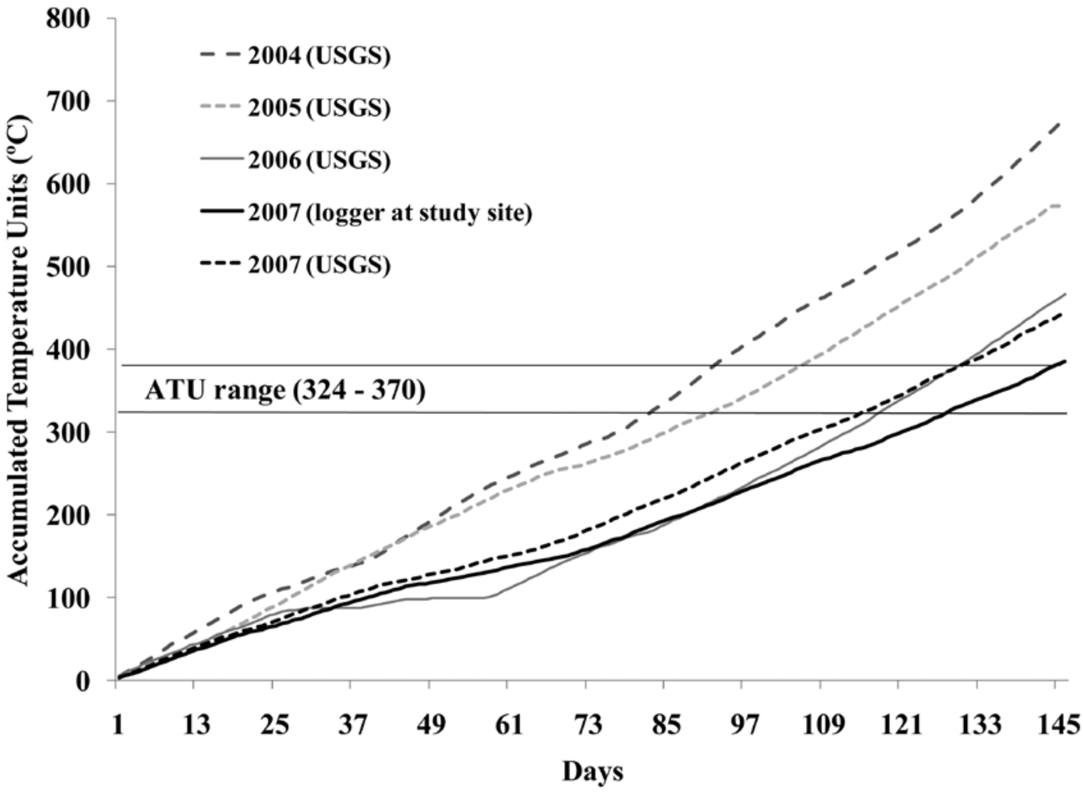

Figure 3. Accumulated temperature units (°C) to hatch during pygmy whitefish egg incubation based on stream temperature data recorded at USGS gage (12115000) in the Cedar River (2004 – 2007). Day 0 for all years is assumed to be December 11. Note that additional data for 2007 were recorded with a HOBO temperature logger at the incubation study site.

116 of the study, but were only slightly warmer than 4 °C by Day 147 when the study concluded (Figure 3). Using the presence of alevin as a definitive indicator of hatching, our results suggest that the majority of eggs hatched between 324 and 370 accumulated temperature units (ATUs) of development under natural riverine conditions.

Daily summary data from the USGS gage (12115000) located near our study site shows considerable inter-annual variability in winter stream temperatures that would affect the timing to hatch of pygmy whitefish eggs. Using 324 to 370 ATUs (this study) as the range of pygmy whitefish hatching, we would retrospectively predict that pygmy whitefish hatching would begin on Day 83 at the earliest and end Day 142 (as in this study) at the latest (Table 2). The average day of hatching at 324 ATUs for the last ten years in the Cedar River was Day 103, corresponding to the middle to end of March.

TABLE 2. Predicted date of hatch for pygmy whitefish eggs based on stream temperatures collected at USGS streamflow-gaging station (12115000) in the Cedar River for years 2000 – 2009.

Year	Days to reach cumulative temperature units (°C) 324 ATUs	370 ATUs	Estimated Hatch Date
2000	97	108	3/17 – 3/28
2001	103	114	3/23 – 4/3
2002	105	117	3/25 – 4/6
2003	91	102	3/11 – 3/22
2004	94	104	3/14 – 3/24
2005	83	91	3/3 – 3/11
2006	92	104	3/12 – 3/24
2007	118	128	4/7 – 4/17
2008	129	142	4/18 – 5/1
2009	123	136	4/13 – 4/25
Average	*103.5*	*114.8*	*3/23 – 4/4*

Discussion

Pygmy whitefish consistently spawn in early December in the Cedar and Rex rivers, major tributaries of CML when temperatures for incubation are coldest (SPU unpublished data). In fact, temperatures are often below 4 °C at these spawning sites. As suggested by Price (1940), whitefish incubate and hatch most successfully at cold temperatures. Selection of spawning habitat providing these low temperatures is thus critical to proper physiological development of eggs. Cold temperatures, however, prolong development, as we found that pygmy whitefish require a relatively long incubation period (127 to 145 days) before hatching as compared to other broadcast spawning species that use freshwater habitats. For example, redside shiners spawn in spring months and required only three to seven days to hatch at 21 °C (Wydowski and Whitney 2003), while shorthead sculpin hatched under laboratory conditions in 29 days at 10 °C. White sturgeon (*Acipenser transmontanus*), another broadcast spawning species utilizing riverine habitat, deposit eggs during spring months and eggs hatch a mere seven days later (Wydowski and Whitney 2003). Because pygmy whitefish deposit eggs during the winter when stream temperatures are coldest, eggs require a substantial amount of time to develop as shown in this study, during which eggs are exposed to potential scouring flows.

Although habitat in the Cedar and Rex rivers provides cold, well oxygenated conditions for developing embryos, use of this spawning habitat does not come without substantial risk during the incubation period, especially to a broadcast spawner like pygmy whitefish. Pygmy whitefish eggs are deposited within an extremely narrow temporal range (approximately two weeks) during early December. Presumably, the eggs are scattered over gravels and settle into interstitial spaces adhering to rock surfaces where they incubate. One benefit of spawning in flowing water is that eggs are more easily dispersed over the gravels rather than concentrated in a single location, which would more likely occur if pygmy whitefish were to spawn in a pelagic environment with little to no flow. For example, use of riverine spawning sites by broadcast spawners might lead to reduced occurrence of fungal infection on eggs simply by spreading eggs over a wider area where they are not in direct contact with each other (Parsley et al. 2002). In addition, predation on eggs from sculpin or other predators could be reduced by scattering eggs over a larger area.

Eggs deposited by riverine spawning pygmy whitefish require several months of incubation before hatching. Our results show that pygmy whitefish hatched (as evidenced by the presence of alevin) over a range of 324 to 370 ATUs under relatively natural conditions (using site-specific stream temperature data)., which was similar to the 348 ATUs found in a previous laboratory study (Price 1940) . Lake whitefish in another study (Brooke 1975) took much longer to reach hatching than pygmy whitefish in this study (446 ATUs at 4 °C). Observed differences between the studies could be attributed to subtle differences in development timing for each study population as well as laboratory versus natural conditions. Although laboratory studies provide highly controlled settings, fish populations have adapted egg development rates under natural flow and thermal regimes encountered in their natal stream (Beacham and Murray 1989) and variation in hatch timing is expected based on local conditions.

The peak period for hatching in this study was Day 134 (346 ATUs), when the highest number of alevin were counted and after which the number of intact eggs sharply declined. Egg membranes were first noted on Day 79 (179 ATUs), but were not conclusively linked to hatching by the presence of alevin. It is possible that the eggs hatched or, alternatively, that they were predated by invertebrates that managed to crawl inside egg boxes. The latter explanation is unlikely because of the fine screening inside each box, and supports the conclusion that 324 ATUs is a conservative estimate of the earliest hatching especially at the southern margin of the species range.

Examination of stream temperatures over a ten-year period in the Cedar River during pygmy whitefish egg incubation shows that 324 ATUs, the conservative beginning of pygmy whitefish egg hatching, occurs on average 103 days after spawning, which would fall on March 23 (assuming December 11 as the average spawning date). Individuals hatch into early April, resulting in some variation in the timing of emergence and movement of young pygmy whitefish into CML. Eggs are spawned over a 2 km reach of stream in both the Cedar and Rex rivers and experience unique temperature conditions at each microsite during development due to groundwater inputs, localized snow and ice accumulations causing cool conditions, and local upwelling processes, adding more variability to the actual timing of hatch for the cohort. The data collected at the study site is located only 100 m upstream from the USGS gage (12115000), yet subtle differences in temperature accumulate over the incubation period and contribute to increasing the range of hatch dates for the cohort as shown by data. Populations at the northern portion of the species range experience prolonged colder temperatures later in the egg development process and may require a longer time to hatch than the CML population. Little information on spawn timing for northern populations exists, but these populations may compensate for colder early spring temperatures by spawning earlier in the calendar year than the CML population (e.g., Heard and Hartman 1966). Incubation conditions vary greatly throughout the species range and variability in hatch timing is expected just as studies have reported for Pacific salmon species in western North America (Beacham and Murray 1989).

Numerous studies on Pacific salmon show that variability in hatch time can be influenced by egg size and female body size where stock-specific egg characteristics can confer different survival rates (Beacham and Murray 1985, 1987, 1989). Subtle differences in pygmy whitefish egg characteristics (e.g., egg size) may contribute to variability in hatch timing and were not accounted for in this study. Furthermore, Konecki et al. (1995) determined that Coho salmon (*Oncorhynchus kisutch*) eggs from a single family hatched over a range of 1–3 weeks demonstrating that variability in hatch timing for eggs of a single female can be relatively wide. No effort was made to determine inter- or intra-female variability in egg incubation timing during this study and the results of this study reflect egg development from a relatively small number of females (n = 24). As these studies suggest, some of the variability observed in hatch timing for pygmy whitefish is likely attributable to natural inter-female variation as well as variation within a family.

In addition, some of the variability in hatch timing observed in this study is likely the result of multiple selection pressures on embryonic and young pygmy whitefish. For example, later hatching individuals may emerge and flush into the reservoir system as zooplankton populations become more plentiful, thereby entering the system with a better food base than was available for earlier hatching juvenile fish. Alternatively, earlier hatching individuals may emerge from the gravels and move out of the river system before being subjected to predation by increased foraging activity by riverine salmonid populations. However, by spending more time in the gravel, later hatching individuals prolong the period when they are at risk of scour from high flow events. Mountain whitefish were observed emerging from substrate at about 14 mm length in late April in the Fraser River (McPhail and Troffe 1998), a time very similar to that predicted for pygmy whitefish in our study. Variation in hatch time for these riverine spawners is important to reduce the risk of one single environmental factor impacting an entire year's cohort.

Predictions of regional effects of global climate change in the Pacific Northwest suggest that warmer winters may result in less winter precipitation falling as snow and more as rain, with potential increases in the frequency of high flow events, (Battin et al. 2007, Mote et al. 2008, Lawler et al. 2010). Consequently, the CML pygmy whitefish population may be at greater risk if flows such as those that occurred during January 2009 on the Cedar River (156 m^3s^{-1}peak flow recorded at USGS gage 12115000 located within the primary pygmy whitefish spawning habitat) occur with greater frequency. Shellberg et al. (2010) found that scour to depths of 10 cm occurred on the Cedar and Rex rivers when discharge exceeded the 2-year recurrence interval (78 m^3s^{-1}). If flows like the January 2009 event, which has an approximately 10-year recurrence interval, were to occur on a more frequent and consistent basis, individual reproductive success could be substantially reduced as most pygmy whitefish do not exceed eight years of age (Wydowski and Whitney 2003, SPU unpublished data), and the CML pygmy whitefish population demographics may change. Increases in the frequency, magnitude, or timing of high flow events may also result in changes in the timing of early development in this population, as selection for shorter development periods may become stronger. Our study has contributed to a better understanding of early development in pygmy whitefish, which can help in developing future management strategies for preserving populations of this interesting and vulnerable species, particularly in the face of potential threats from the effects of climate change.

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